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Cavers' knowledge of biosecurity and its influence on the prevention of white-nose disease

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Abstract

White-nose disease (WND) is a deadly disease in hibernating bats. Its causal agent is the fungus *Pseudogymnoascus destructans* (*Pd*) that was only recently introduced to North America, where it causes pervasive mortality. In contrast, it is native to Eurasia, where bats do not experience mass mortality. The pathogen successfully survives for long periods in cave substrates (e.g., mud, soil) as well as on contaminated caving clothes and equipment. This emphasizes the importance of limiting its human-mediated spread, particularly over long distances and from areas where it is native and genetically highly diverse. To assess associated conservation risks more precisely, we conducted a global online survey on cavers' WND knowledge, travel frequencies, and hygiene habits regarding caving equipment, and we analysed the relationship between those variables. We interpreted our results based on respondents' continents of origin, separating them into 3 categories: continents where *Pd* was recently introduced and continues to cause significant bat mortality (North America); continents where *Pd* is currently not present but is hypothesized to cause bat mortality if introduced (Australia and South and Central America); and continents where *Pd* is native and currently not associated with bat mortality (Europe and Asia). We found significant differences between categories, showing that further awareness of WND is most needed in Europe and Asia where specific guidelines for limiting *Pd* spread are still to be developed. Interestingly, however, WND knowledge alone explained very little variance in respondents' hygiene habits, showing that other factors such as habits, emotions, or personal values have a stronger influence on cavers' behaviour.

Keywords
Bat conservation, pathogen pollution, *Pseudogymnoascus destructans*, white-nose syndrome, wildlife disease

Introduction

White-nose disease (WND), or white-nose syndrome as it is often referred to (WNS, please see (Whiting-Fawcett et al. 2025 for details on nomenclature), is a deadly disease in hibernating bats that has caused population declines of more than 90% in the colonies of most affected bat species in North America (Cheng et al. 2021). Its causal agent is the cave-dwelling and cold-loving fungus *Pseudogymnoascus destructans* (*Pd*), native to Eurasia and only recently introduced to North America, most likely by humans (Leopardi et al. 2015; Drees et al. 2018), providing a notorious example of pathogen pollution. This recent introduction explains the pervasive mortality due to WND in North America and the lack of mass morbidity or mortality in Europe (Puechmaille et al. 2010, 2011; Zukal et al. 2016; Fritze and Puechmaille 2018). Importantly, *Pd* only infects bats during hibernation, when their body temperature is low enough to allow the growth of a psychrophilic pathogen, but it is able to survive for multiple years in the substrate, making caves its environmental reservoir (Puechmaille et al. 2011; Fischer et al. 2020, 2022; Hoyt et al. 2020). This has two major consequences. First, healthy bats can get infected anew each autumn when they return to their hibernacula (Puechmaille et al. 2011; Hoyt et al. 2021; Fischer et al. 2022; Hicks et al. 2023; Zhelyazkova et al. 2024). Second, the unintentional transportation of cave substrate (e.g., via dirty clothes and equipment) can spread *Pd* spores, and therefore introduce the pathogen to new sites, countries, or continents. It can also move the pathogen between existing populations, creating favourable conditions for genetic mixing of previously isolated entities, which might lead to the emergence of potentially more dangerous pathogen variants, as classically encountered in fungi (Brasier and Buck 2001; Stukenbrock 2016).

In North America, where subterranean habitats are still in the process of *Pd* colonisation, bats have proved to be important vectors of its spread over short distances (e.g., Maher et al. 2012) as the fungus can only survive for several days on normothermic animals (Campbell et al. 2020). Additionally, tracking individual *Pd* genotypes in Europe has demonstrated very limited movement and/or establishment of the pathogen to already colonized sites within its native range of occurrence (Fischer et al. 2022). Together, these findings show that, although inevitable, "natural" bat-mediated *Pd* spread is relatively slow and subject to significant long-term limitations. In contrast, thanks to modern means of transportation and the ever-rising popularity of international travel, people effectively act as fast long-distance *Pd* vectors, even across continents. Thus, both the transcontinental introduction of the pathogen from Europe to North America (Leopardi et al. 2015) and its introduction from the East to the West Coast of the US (Lorch et al. 2006; Thapa et al. 2021) are considered human-mediated. The same is most probably true for *Pd* spread in other large countries such as Russia or China. Importantly, it was demonstrated that *Pd* spores not only easily stick

to caving equipment after visiting a *Pd*-positive subterranean sites but can survive on such contaminated equipment at room temperature for at least 25 days (Zhelyazkova et al. 2020). This means that risks of human-mediated pathogen introductions remain even when pauses between trips are made.

Considering all of the above, raising WND awareness is thought to be a successful strategy to reduce the long-distance spread of *Pd* and possibly other cave microbes. Yet, very little has been published regarding the effectiveness of such information campaigns and the different factors that might influence cavers' behaviour. For example, Salleh et al. (2021) analysed WND knowledge and cleaning habits among the participants in a speleological conference in Australia and Shapiro et al. (2022) surveyed people's attitudes and behavioural intent towards WND prevention measures applied by US National Parks. Thus, the results of these studies are biased towards people who are already interested in cave conservation and/or come from continents where WND is causing or expected to cause bat mortality (North America and Australia) (Blomberg et al. 2023). However, new *Pd* (re-)introductions are not less probable from places where the pathogen is currently not causing bat mortality (e.g., Europe and Asia), thus effective WND prevention can only be achieved by a global approach. As a step in this direction, we conducted a global online survey on cavers' WND knowledge, travel frequencies, and hygiene habits, and we analysed the relationship between those variables. We used a broad definition of "cavers" referring to any people practicing any activities in natural caves of various origins, as well as mines and other artificial underground sites. We interpreted most of our results based on respondents' continents of origin separating them into 3 categories: continents where *Pd* was recently introduced and continues to cause significant bat mortality (North America); continents where *Pd* is currently not present but is hypothesized to cause bat mortality if introduced (Australia and South and Central America, see Escobar et al. 2014; Turbill and Welbergen 2020; Blomberg et al. 2023); and continents where *Pd* is native and not associated with bat mortality (Europe and Asia). We hypothesized that WND knowledge would be higher at places seriously affected by the disease and that this knowledge would exert a strong influence on cavers' hygiene habits.

Methods

Survey design and distribution

The study was a cross-sectional qualitative survey carried out entirely online with no restriction regarding participants' countries of residence. The questionnaire was designed by the authors and consisted of 23 questions divided into the following sections: 1) Caving (including hygiene) habits, 2) Knowledge of white-nose disease, 3) Willingness to change caving habits for conservation purposes, and 4) Demographic data. Eighteen questions had multiple-choice answers, three of which allowed an open answer and four of which allowed multiple answers; two questions required numerical input; and three required entirely open answers (see Suppl. material 1 for the full

questionnaire). At the end, participants were invited to share their opinions in a free form and enter their e-mail addresses in order to receive information about the study results. The questionnaire was uploaded to a specifically created website (https://washyoursuit.batspa.org/) where it was available in seven languages: English, Spanish, French, Chinese, Russian, Slovenian, and Bulgarian. It was open between the 6th of May and the 6th of August 2021. People were invited to fill it out using the mailing lists of national and international speleological federations and several international bat research groups (see Suppl. material 2 for the full list of these organisations) as well as via posts on social media. Additionally, all authors distributed the questionnaire among their personal contacts. Distributing the questionnaire was approved by the Ethical Commission at the National Museum of Natural History Sofia. We adhered to the European law for General Data Protection Regulation (GDPR) (http://data.europa.eu/eli/reg/2016/679/oj).

Data formatting

The survey was conducted using the online software 1KA (https://1ka.arnes.si/) developed by the Centre for Social Informatics at the Faculty of Social Sciences at the University of Ljubljana, Slovenia. The obtained data was then exported as a '.csv' file and further analysed with the R software v. 4.3.2 (R Core Team 2023) using the tidyverse collection of packages (Wickham et al. 2019). For building the graphs, we also used the packages cowplot (Wilke et al. 2024), viridis (Garnier et al. 2024), ggpubr (Kassambara 2023), and ggsankey (Sjoberg 2024). Responses were considered for analysis if all survey questions were answered. Unfortunately, the two respondents from Africa were not analysed due to the very low sample size for this continent.

Cavers' hygiene habits were assessed separately for 4 travel distances from the respondent's home to the particular cave (0–100 km, 101–1000 km, 1001–5000 km, and >5000 km; Q5) as these bring different levels of conservation risks. More precisely, we consider 0–100 km as the only distance presenting low conservation risk as inferred from usual movement distances of *Myotis myotis* (https://jasja.shinyapps.io/ClimBats/), the most common host of *Pd* in Europe, possibly providing means for the natural spread of the fungus. Another evidence for such natural spread comes from genetic research in Germany and Bulgaria, where we found very limited shared *Pd* genotypes between hibernacula situated within 21–83 km of each other and no shared genotypes between hibernacula situated 300 km from each other (Fischer et al. 2022; Zhelyazkova et al. 2024). Then, we consider all other distances as presenting higher conservation risks, where 101–1000 km approximates travelling within countries; 1001–5000 km approximates travelling between countries; and > 5000 km approximates travelling between continents.

For statistical analyses, we converted hygiene habits for each travel distance to numbers by giving a numerical score of each equipment cleaning method according to its effectiveness at eliminating *Pd*. Thus, we defined our cleaning score according to the following scheme: 1 = "Do not clean"; 2 = "Clean with water only"; 3 = "Clean with water and soap/another detergent"; 4 = "Disinfect/decontaminate". Respondents who had

marked more than one cleaning method for the same travel distance were given an average cleaning score. Then, we defined our biosecurity score as equal to the cleaning score when respondents only used their personal equipment when travelling, or as an average between the cleaning score and 5 when respondents had marked both the option of bringing personal equipment and renting/borrowing local equipment (Q4). Respondents who always borrowed/rented local equipment were given a biosecurity score of 5.

To assess overall knowledge of WND and its causative agent, we used the total number of correct answers to the 7 related questions (Q6 to Q12, see Suppl. material 1), where each correctly answered question earned 1 point. Questions that allowed multiple answers received a full point when respondents had chosen all the correct and none of the wrong answer options and n/N points where n is the number of correct answer options and N is the total number of answer options. Responses regarding *Pd* distribution were assessed as correct or wrong based on the relevant publications that were available at the time the questionnaire was open (Suppl. material 3).

Data analysis

To check for consistency in cavers' hygiene habits across distances, we performed a permutation test (Nperm = 1000) where we randomised answers given by the same people regarding equipment cleaning preferences when travelling different distances. This gave us the number of respondents that would have the same biosecurity scores for each travel distance by chance and we compared it with the actual number of respondents having the same biosecurity score for each travel distance. Additionally, to investigate tendencies in hygiene habits to change among cavers, we selected only respondents with different biosecurity scores for the different distances, and we performed a linear model with biosecurity score as the dependent variable and travel distance as the explanatory variable. Prior to both tests, we selected respondents who make a trip at each of the four distances at least once per year.

To study factors that might influence cavers' hygiene habits, we chose biosecurity scores for the travel distance 101–1000 km as it represents the largest number of travels documented for a distance that goes beyond the natural spread distance of *Pd*. Then, we performed hierarchical linear regression with biosecurity score as the dependent variable and: purpose of caving activities; number of annual caving trips; WND-knowledge (expressed as the total number of correct answers to the 7 related questions); exposure to information related to the human impact on cave ecosystems; behavioural change as a result of receiving such information; continent of residence; age; years spent at school; years of caving experience; and caving club membership as explanatory variables (see Suppl. material 1 for the exact questions). We then repeated the same analysis only on participants who had heard of WND, where we used adherence to WND-related instructions, participation in WND-related studies, and attitude towards limiting anthropogenic *Pd* spread in addition to the explanatory variables listed above. We used the MASS package (Venables and Ripley 2002) for automatic model selection based on the Akaike information criterion and the moments package (Komsta and Novomestky

2022) for calculating the skewness of model residuals. Outliers in the biosecurity score data were removed in order to satisfy the assumption of normality of residuals necessary to perform linear regression analyses. This resulted in omitting 7 observations in the case when all respondents were considered and 4 observations in the case where only respondents who had heard of WND were considered.

For analysing the differences in WND knowledge between people practicing different types of caving activities, we used ANOVA and Tukey's HSD test.

The original master data and the R script used for the analysis are provided in Suppl. materials 7–11.

Results

Survey participants

A total of 654 cavers completed the whole survey and were included in our analysis. These came from 43 countries (Suppl. material 4) on 5 continents and used all the proposed languages except Chinese. Demographic data as summarised in Fig. 1 depict a diverse respondents' population.

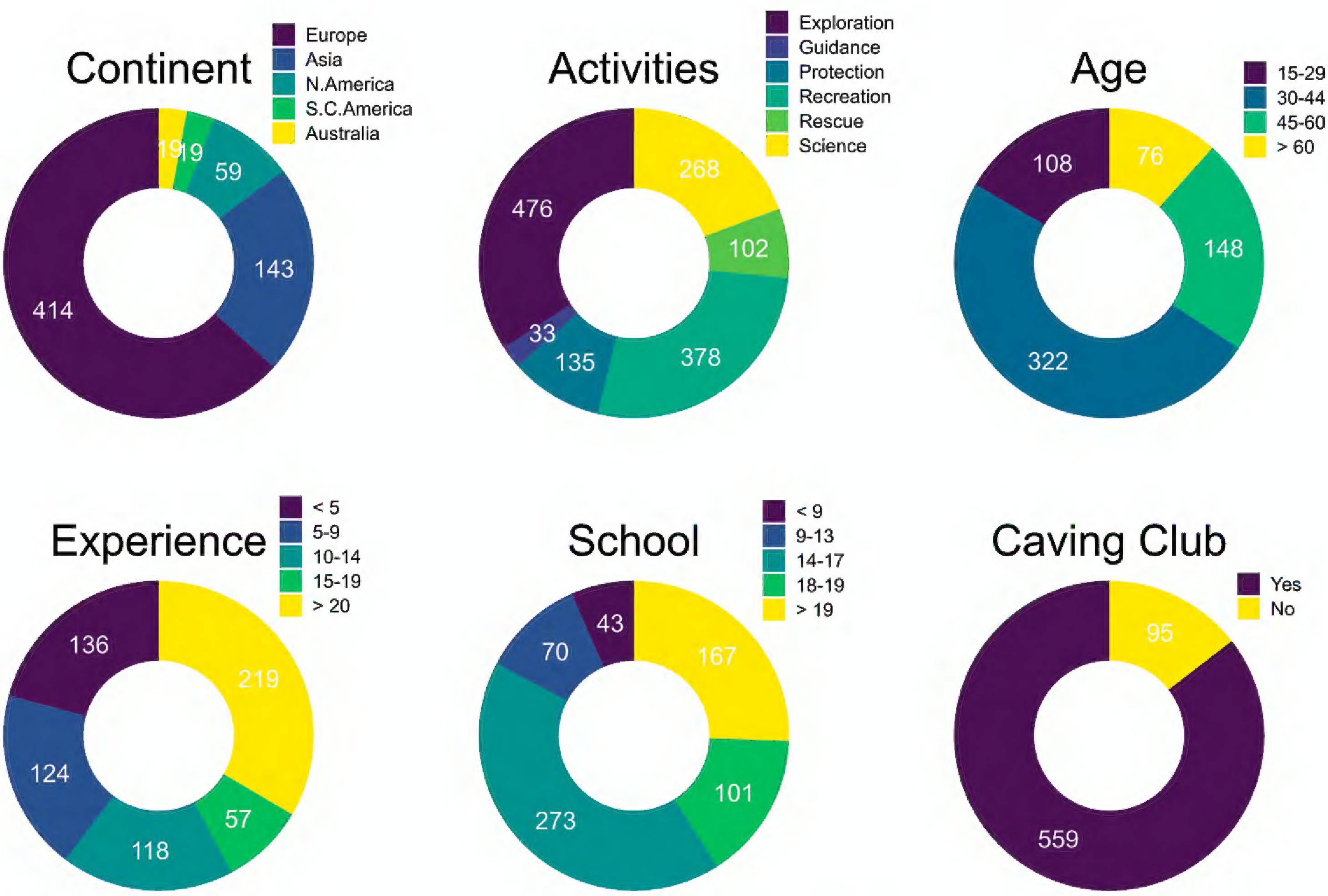

Figure 1. Demographic data of survey participants. Continent of residence, purpose of caving activities, age, years of caving experience, years spent at school (including university), and membership in a caving club or a similar organisation are shown. The sum of people practicing different caving activities is higher than the total number of participants as multiple answers were allowed for this question.

Caving travel frequency

Not surprisingly, people visit caves situated closer to their homes more often than caves that are far away. Almost 40% of our respondents visit a cave up to 100 km from their homes at least once per month and 14% pay a monthly visit to a cave situated between 100 and 1000 km from their homes. Thirty-two percent of respondents travel for caving at distances between 1000 and 5000 km at least once per year and 14% annually visit a cave at a distance of more than 5000 km (Fig. 2). Divided by continent, Europeans report to travel more often at distances up to 100 km, while Americans travel more often at distances up to 5000 km (Fig. 2). These results, however, should be interpreted with caution as some of these differences may be due to differences in sample sizes of respondents from different continents (Fig. 1, Suppl. material 4).

Cavers' hygiene habits

Cavers' hygiene habits differ across continents (Fig. 3). Respondents from Europe and Asia prefer to clean their personal equipment (e.g., caving suits, boots, harnesses, etc.) with water only, while those from South and Central America and Australia prefer using water and soap. Cavers from North America most often adhere to WND decontamination procedures.

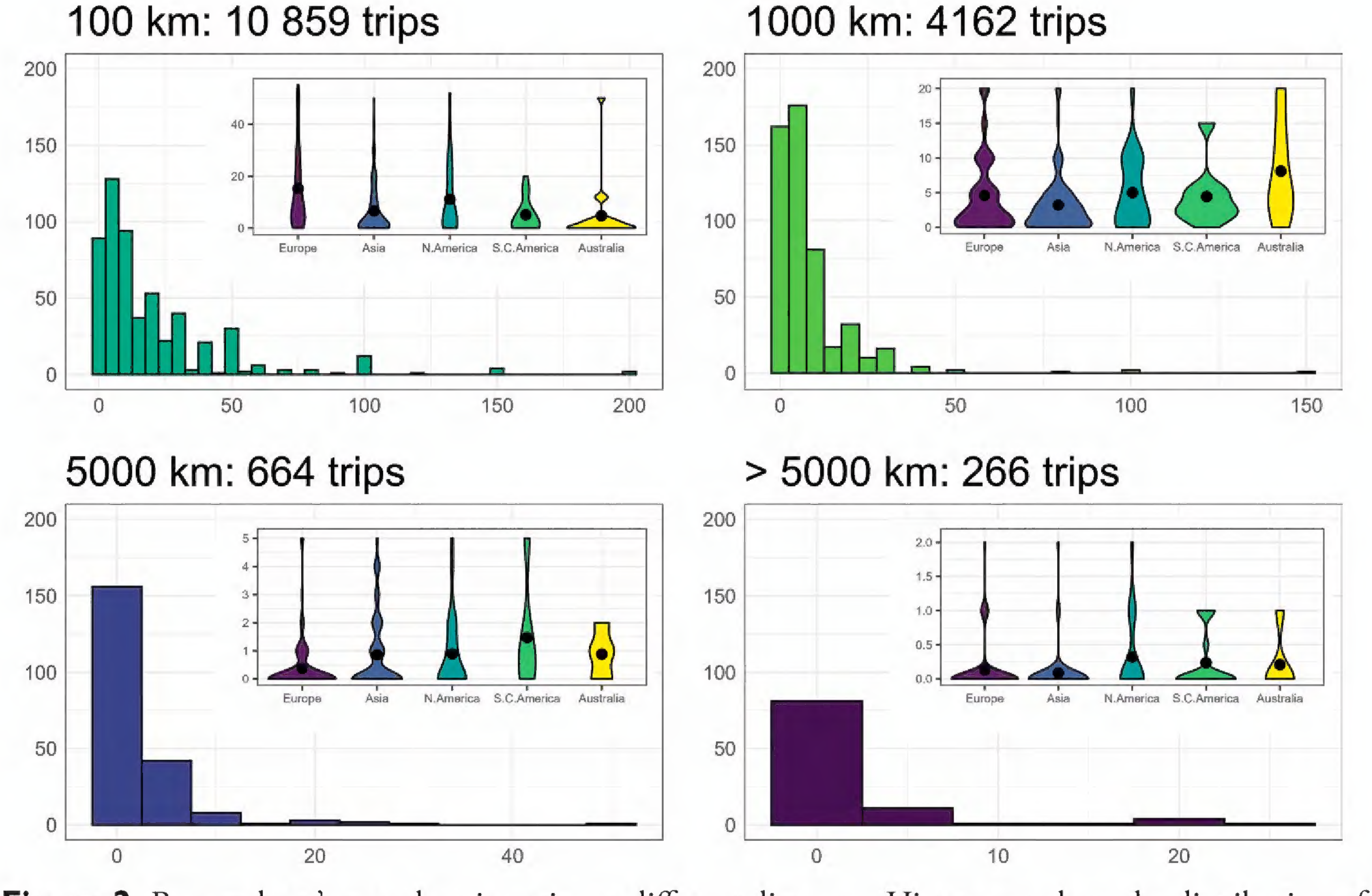

Figure 2. Respondents' annual caving trips at different distances. Histograms show the distribution of all respondents (y-axis) taking a certain number of trips per year (x-axis). The total number of trips by all people from all continents is shown in the title. Violin plots show a summary of annual caving trips per person for each continent, where the dot shows the median of the data.

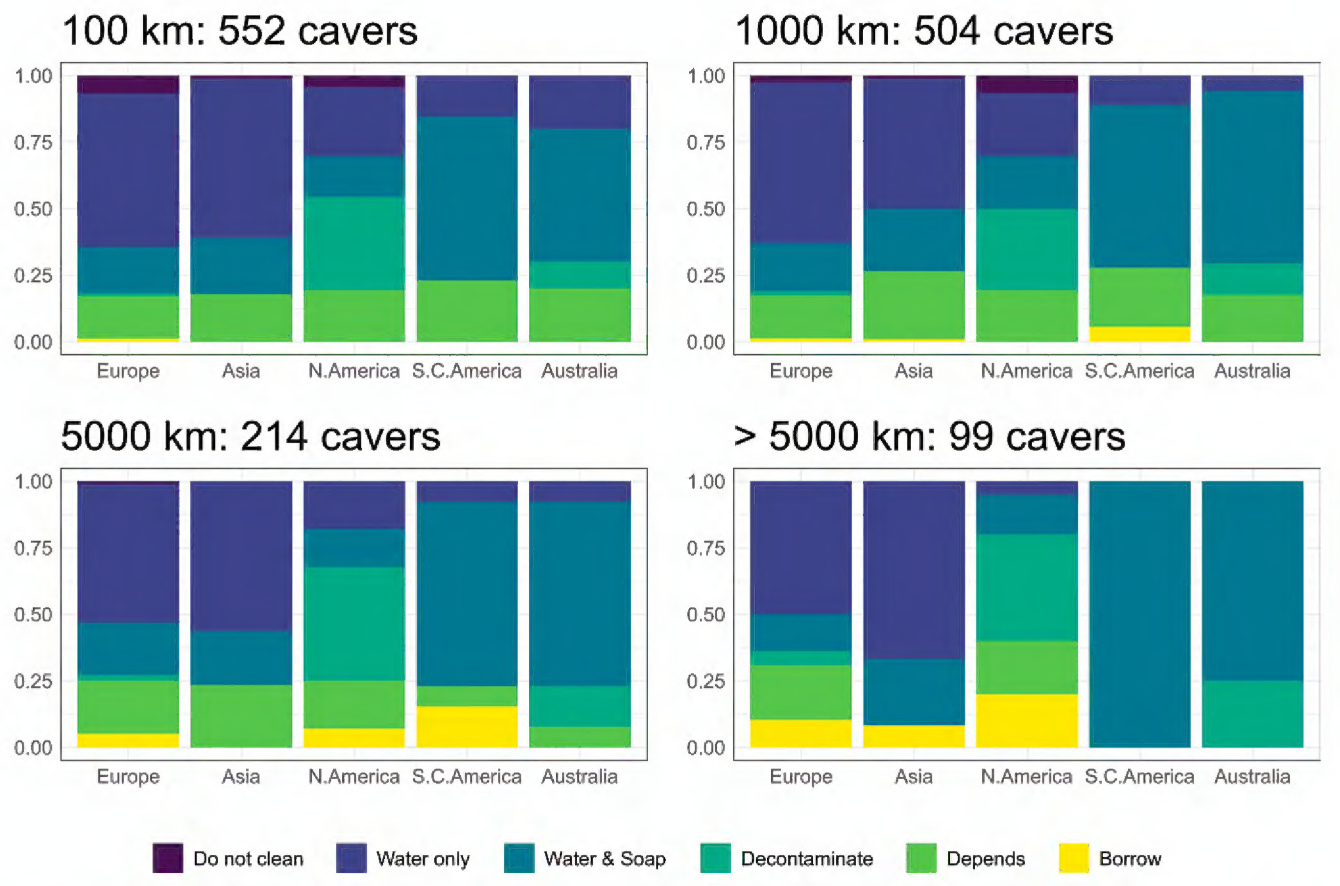

Figure 3. Cavers' hygiene habits on different continents. These are shown as percentages of the total number of people from each group that travel at the corresponding distance at least once per year. This number is given in the titles. The answer "Depends" unites respondents who marked more than one cleaning method and/or both use personal or locally borrowed equipment.

If we only consider cavers that travel all distances (n = 63), 54% are consistent in their hygiene habits. Those changing habits with distance (46%) show a tendency for cleaning procedure improvement (Suppl. material 5).

Cavers' WND knowledge

WND knowledge, adherence to WND-related instructions, and participation in WND studies also differ on different continents (Fig. 4). Cavers from North America know most about the disease and most often follow specific instructions for its mitigation. Cavers from South and Central America and Australia are also well aware of WND and a good fraction of them follow WND-related instructions. In contrast, cavers from Europe and Asia are poorly informed about WND and rarely pay efforts to prevent its further spread (Fig. 4).

According to AIC, the best linear model explaining cavers' hygiene habits when all respondents are considered is the one containing continent of origin, WND knowledge, and age as explanatory variables, with age providing barely noticeable difference in AIC. When only respondents who have heard of WND are considered, the best model included continent of origin, adherence to WND-related instructions, and participation in WND studies. In both analyses, the continent of origin explains most of the variance in biosecurity scores and WND knowledge only weakly improves the model (Table 1; Suppl. material 6).

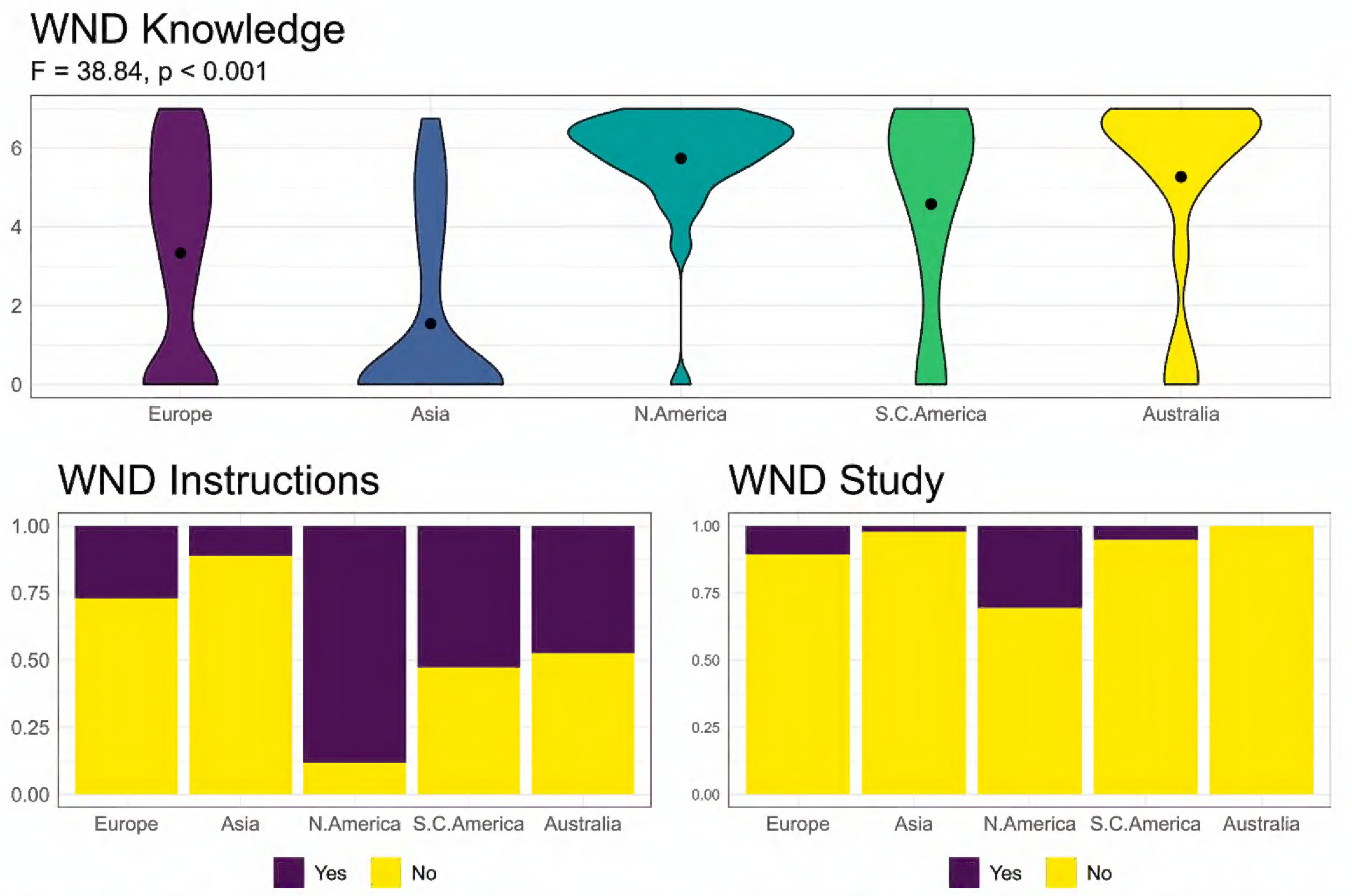

Figure 4. Differences in WND knowledge, adherence to WND-related instructions and WND-study involvement among cavers from different continents. WND knowledge is expressed as the total number of correct answers given by respondents from each continent, where the dot shows the median of the data. Adherence to WND-related instructions and WND-study involvement are shown as percentages.

The most common reason for cavers to follow WND-related instructions is their own sense of responsibility, and the most common reason for not following them is lack of awareness. The majority of respondents who have heard about WND have a positive attitude towards limiting anthropogenic *Pd* spread and the majority of respondents who have received information related to the human impact on cave ecosystems have changed their behaviour in response (Fig. 5).

Transcontinental travel and associated conservation risks

After being asked to click up to 10 locations on a map where they have been caving for the past 10 years, our respondents reported a total of 387 trips between continents. Out of these, 137 trips have been made by cavers (n = 69) who clean their equipment only with water or do not clean it at all (biosecurity score for trips 1001–5000 km < 2.5 or biosecurity score for trips > 5000 km < 2.5), including from Europe to North America and Australia (Fig. 6A). A considerable fraction of these respondents is unaware that *Pd* can be found on used caving equipment and/or believes the pathogen is not present in their country of residence; yet, some respondents are aware of WND-associated risks and still do not thoroughly clean their equipment.

Table 1. Factors that best explain cavers' biosecurity scores as shown by hierarchical linear regression. The analysis included the following steps: 1) running linear models using biosecurity scores as a response variable with all possible combinations of explanatory variables (see M&M section for the full list); 2) automatically choosing the best model based on AIC 3) running a hierarchical linear regression by adding the significant explanatory variables chosen in the previous step one by one in order to differentiate their individual contribution to the model. Thus, the incremental R-squared (Incr R-squared) is the difference between R-squared of the model with and without the newly added variable and shows how much this newly added variable improves the model. Model significance (p-value) is represented in the R-squared column by an asterisk with '***' meaning p < 0.001.

All respondents (n = 504)		
Explanatory variable	R-squared	Incr. R-squared
Continent	0.13***	
Continent + WND-knowledge	0.15***	0.02
Continent + WND-knowledge + Age	0.16***	0.01
Respondents who have heard of WND (n = 350)		
Continent	0.15***	
Continent + WND-instructions	0.20***	0.05
Continent + WND-instructions + WND-study	0.22***	0.02

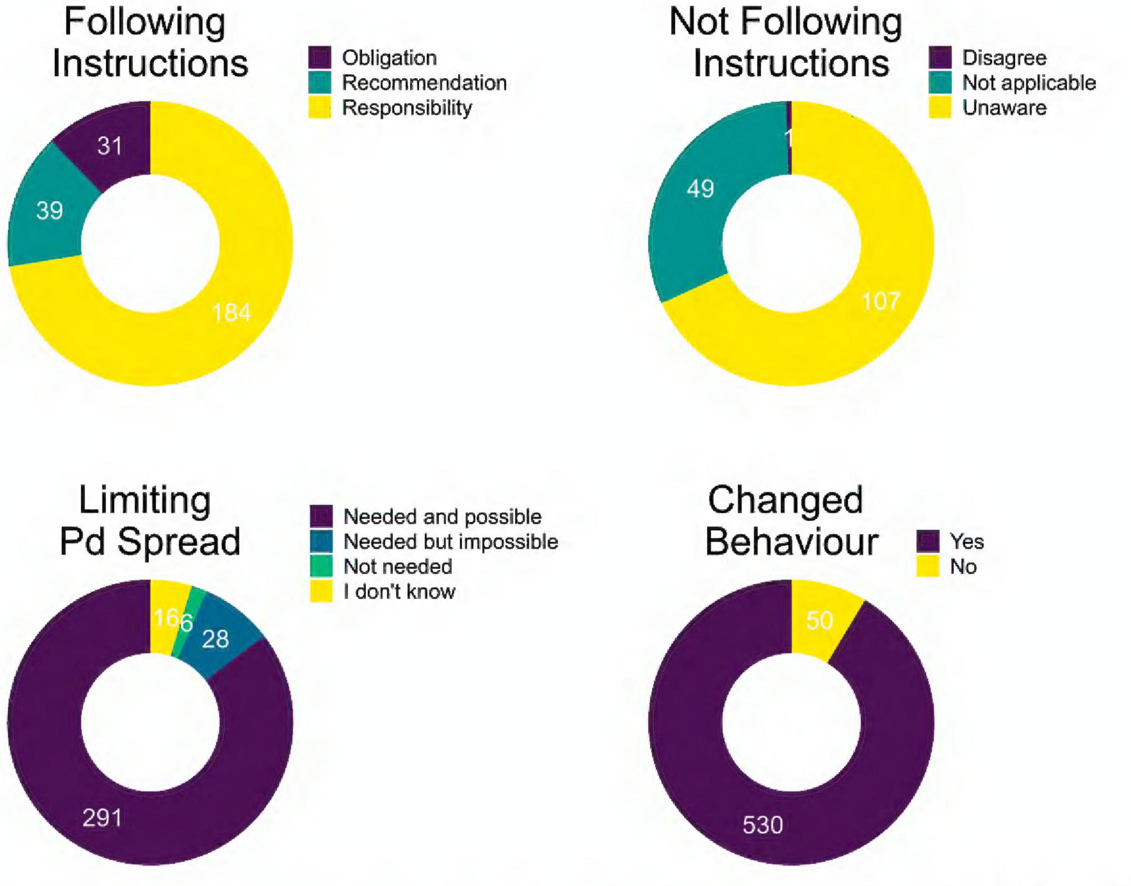

Figure 5. Cavers' motivation to follow or not WND-related instructions, attitude toward limiting anthropogenic *Pd* spread, and willingness to change behaviour after receiving any information related to human impact on cave ecosystems. See Suppl. material 1 for the exact question phrasing.

Of note, 35% of people travelling between continents with low biosecurity scores stated involvement in some scientific activities (Fig. 6B). Additionally, although WND knowledge is significantly higher among cavers practicing science, we observed no significant difference between hygiene habits based on the stated purpose of caving activities (Fig. 7).

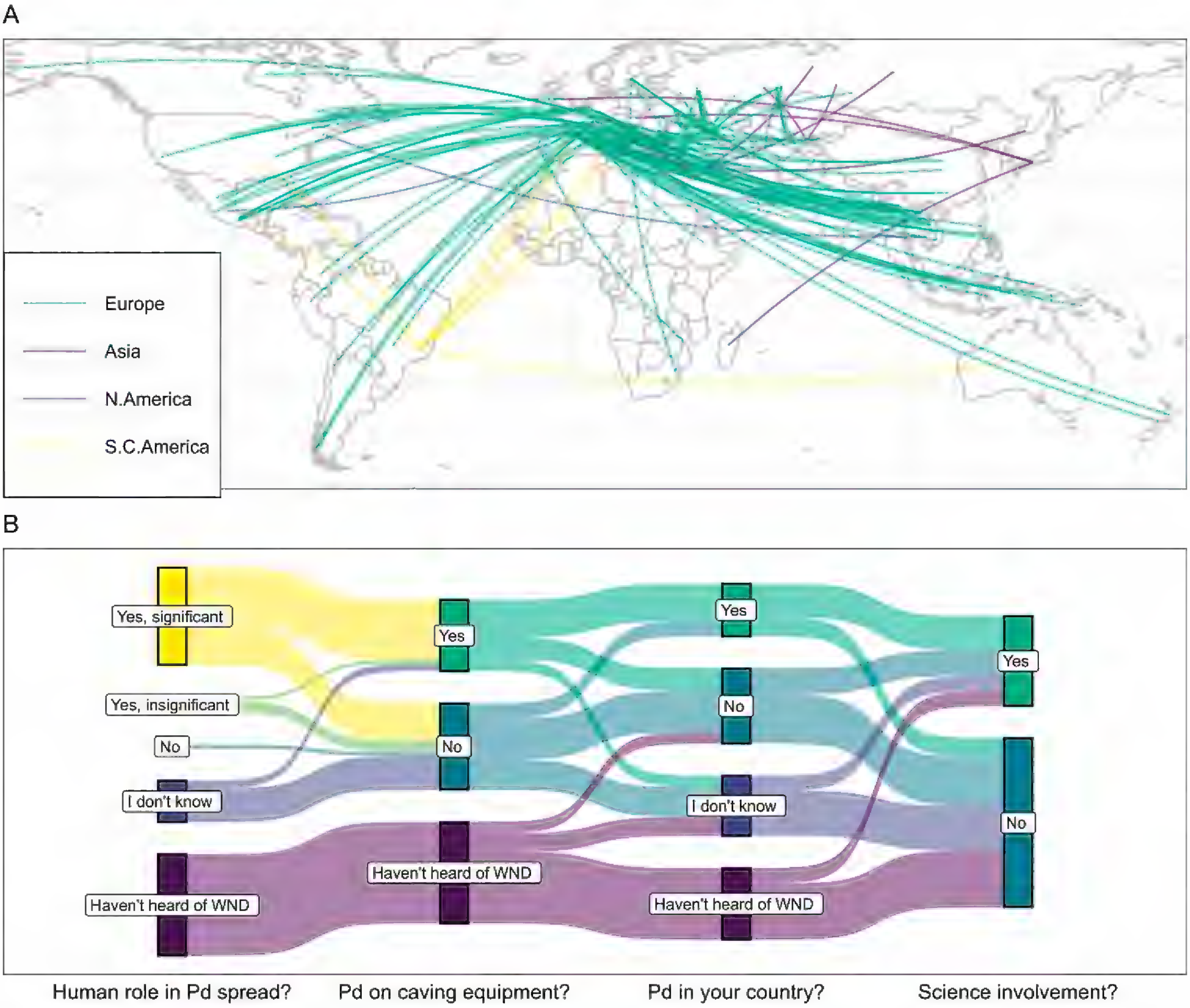

Figure 6. A a map of transcontinental caving trips reported by our respondents for the past 10 years. This is not an exhaustive list as the questionnaire allowed pointing a maximum of 10 locations per respondent. To illustrate risks regarding the spread of *Pd* and other cave microbes, here we only show people with biosecurity scores for trips 1001–5000 km < 2.5 or biosecurity scores for trips > 5000 km < 2.5, meaning they clean their equipment with water only or not clean it at all; **B** analysis of the same respondents showing the most probable reasons for them choosing weak hygiene procedures.

Discussion

In agreement with the first part of our hypothesis, our study showed a large difference in WND awareness, adherence to WND-related instructions and hygiene habits (expressed here as biosecurity scores) between cavers on different continents. In contrast, we did not find a strong support for WND knowledge influencing cavers' hygiene habits by itself, which refutes the second part of our hypothesis. Such results align with the Theory of Planned Behaviour (TPB, Ajzen 1985), which posits that human behavioural intentions are determined by three components. These are: 1) attitude (Do I approve/like this behaviour?); 2) subjective norms (Is this behaviour socially desirable?); and 3) perceived behavioural controls (Do I find this behaviour feasible to me?). Within this conceptual framework, knowledge can indirectly influence behaviour by shaping one or more of these components, yet, habits, emotions or personal values often play a much bigger role. Thus, cavers in North America may be stricter at cleaning

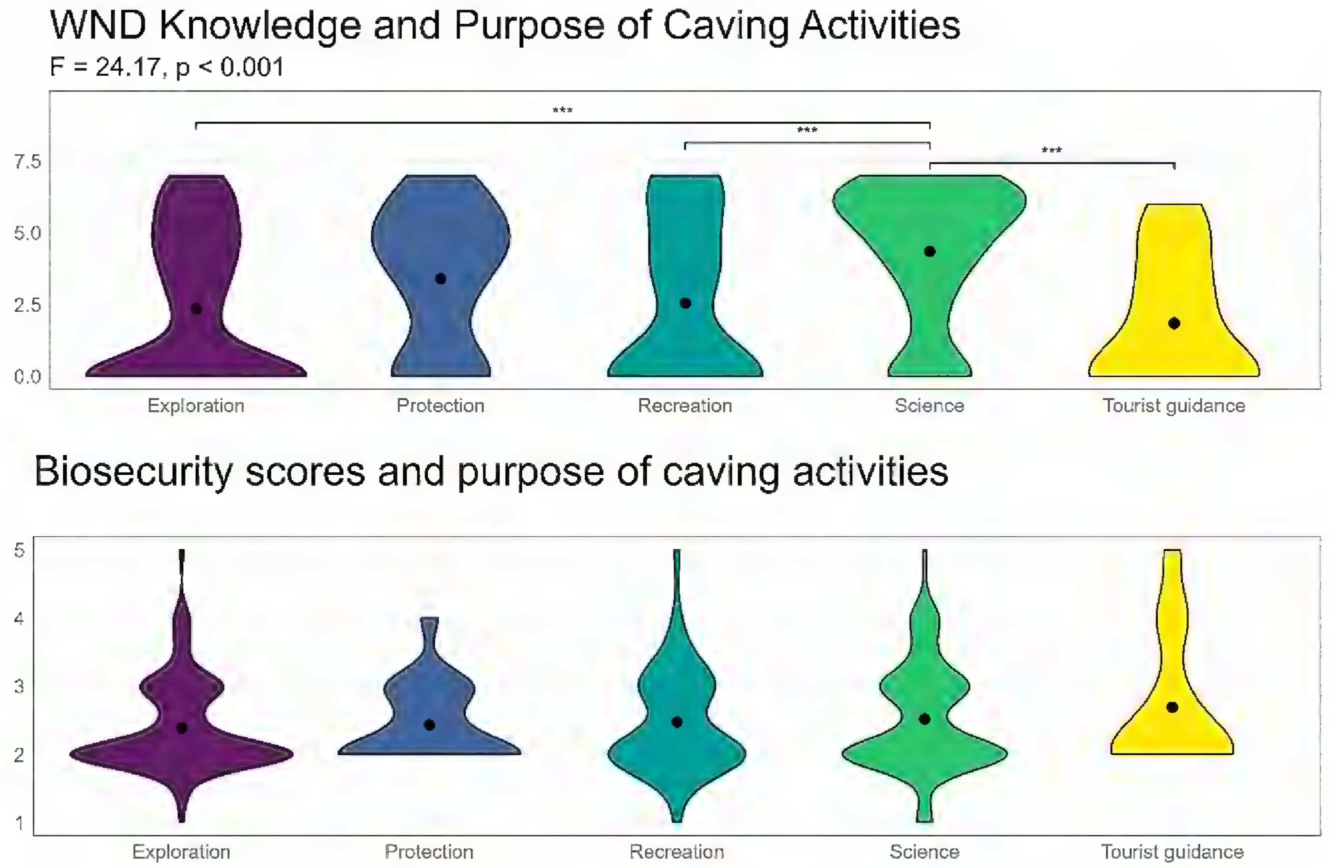

Figure 7. WND-knowledge among respondents practicing different types of caving activities. As multiple answers were allowed for this question, the group "Science" includes people practicing cave science and other activities, the group "Protection" includes people practicing cave protection and other activities except science, the group "Tourist guidance" includes people practicing tourist guidance, cave exploration, and recreational caving, the group "Exploration" includes people practicing cave exploration and recreational caving, and the group "Recreational" includes people practicing recreational caving only. The dot shows the median of the data.

and decontaminating their equipment not only because they are more aware of WND but also for other more personal reasons. For example, the mere sight of hundreds of dead bats during the WND epidemics must have raised empathy and motivation for action among the caving community and the broader society (Component 1 of TPB). Additionally, once WND-related instructions were widely distributed and a certain mass of people started complying to them, it must have become socially desirable to adopt such behaviour (Component 2 of TPB). On the other hand, cavers in South America may wash their caving clothes with soap not necessarily with the intention of pathogen pollution prevention but in agreement with their everyday habits. As people from warmer countries normally go caving with everyday clothes such as pants and a T-shirt, they might find it easy to put these in the washing machine in contrast to cavers from colder countries who use heavy caving suits, often sensitive to detergents. Such behaviour aligns with Component 3 of TPB. Another example of habits' importance is the consistency in cavers' hygiene practices across travel distances. On the other hand, applying stricter cleaning methods when travelling further may be motivated by awareness of the higher conservation risks following long-distance *Pd* spread.

The same theory also explains our seemingly striking observation that cavers practicing science-related activities have better WND knowledge but not better hygiene habits than cavers who are not involved in research. This is so as professional caving for scientific purposes often involves project requirements, deadlines and budget restrictions that may

require visiting multiple caves per trip, sometimes in different geographical regions. The last is especially true for monitoring activities. In contrast, recreational caving is usually practiced within the comfort zone of participants who normally spend a caving weekend within the same geographical region. Thus, cleaning equipment between sites may be generally less feasible during scientific activities the way they are standardly organized.

Yet, our results do not mean that increasing cavers' WND knowledge is useless in WND prevention. On the contrary, although it is not enough to motivate action by itself, knowledge provides the necessary instrumentation to perform a particular behaviour, once it becomes desired. This is exemplified by our results where the main reason for cavers following WND-related instructions is personal responsibility but the main reason for people not following such is the lack of awareness. In this regard, the results of our study provide useful clues on where the gaps in WND awareness are and what might be the reasons for them. Thus, cavers from North America, where *Pd* has been decimating bat populations in the past two decades, are particularly knowledgeable about WND and the specific instructions designed for its mitigation. This is expected given the significant ecological and economic consequences of reduced bat populations due to the disease that motivated the rapid testing and dissemination of *Pd* decontamination protocols (https://www.whitenosesyndrome.org/mmedia-education/national-wns-decontamination-protocol-u-s). Additionally, a variety of information resources such as articles, infographs, short videos, or whole documentaries, was developed and made accessible to the general public (see the Resources tab at https://www.whitenosesyndrome.org/). As evidenced by the high percentage of correct answers to WND-related questions among our North American respondents, these resources seem to have been effective at increasing awareness about the disease. As for continents such as South and Central America and Australia where *Pd* is not yet reported but is expected to cause serious bat morbidity or mortality if introduced, cavers are also well aware of WND, with approximately half of them preventively adhering to some WND-related instructions. In Australia, this is most probably explained by the fact that specific WND-response guidelines have already been developed and disseminated there https://wildlifehealthaustralia.com.au). Additionally, the country has a strict biosecurity policy in general and offers useful information resources to different target groups in order to prevent the spread of invasive pests and diseases (https://www.biosecurity.gov.au/). In contrast, we are not aware of formal biosecurity protocols in South American countries but our data is insufficient to determine whether responses from this continent reflect local conservation campaigns, broader access to information from the US, or simply local climatic conditions. Such local contexts should be taken into account when designing field hygiene protocols.

In Europe and Asia, where *Pd* is currently not associated with bat mortality, cavers are least aware of WND and usually clean their equipment solely with water, which can remove some but not all fungal spores (Zhelyazkova et al. 2020). This is expected both due to the lack of an immediately apparent problem and to the fact that *Pd* was discovered and proven native to Europe (Puechmaille et al. 2010) and Asia (Hoyt et al. 2016) after the disease had manifested in the US. Indeed, some WND-related instructions have been developed in Europe such as the BCI guidance for bat workers in UK (https://cdn.bats.org.uk/uploads/pdf/About%20Bats/WNS/UK-Guidance-for-bat-workers-Nov-2024.

pdf?v=1734025851). However, these do not seem to be so popular in other countries. IUCN has also published detailed guidelines for field hygiene (https://www.iucnbsg.org/guidelines-for-field-hygiene.html), which are particularly valuable for researchers handling bats but not so applicable to recreational cavers. Lastly, the European Speleological Federation has created a WND factsheet containing recommendations for cavers (https://www.eurospeleo.eu/ECPC/wp-content/uploads/2022/09/ECPC_WNS_in_Europe_cavers_ENFR.pdf?), however it dates back to 2010 and does not reflect current advancements of the disease knowledge. Thus, we suggest to continue increasing WND awareness among the Eurasian caving community and to better explain the difference between short- and long-distance *Pd* spread on this continent. More precisely, according to the latest scientific evidence, moving *Pd* between sites in the same geographical region in Europe or Asia (e.g., at distances below 100 km) is indeed associated with minimal conservation risks. This is so as the fungus is already widely distributed (Puechmaille et al. 2011; Zukal et al. 2016; Bloomberg et al. 2023); bats have had sufficient evolutionary time to adapt to it, mostly by developing immunological tolerance (Fritze et al. 2019, 2021; Whiting-Fawcett et al. 2025); and there is probably significant intraspecific competition preventing the establishment of new *Pd* genotypes into new sites already colonized by the same species (Fischer et al. 2022; Zhelyazkova et al. 2024). On the other hand, moving *Pd* between different geographical regions can have negative consequences by facilitating genetic recombination between different strains, potentially leading to the emergence of hypervirulent pathogen variants. This has happened in *Batrachochytrium dendrobatidis*, the causative agent of the deadly chytridiomycosis in amphibians (Farrer et al. 2011). Particularly high attention should be paid to intercontinental travel as it risks introducing *Pd* into previously unaffected areas or increasing genetic diversity in already infected regions, allowing strains previously isolated geographically to interact. While not every trip with *Pd*-contaminated gear will result in the successful establishment of *Pd*, each instance raises the likelihood of its introduction by increasing propagule pressure (Lockwood et al. 2005). Hence it is better to be "safe than sorry" as it has been proven extremely challenging to find efficient management strategies to counter WND: from nearly 200 papers addressing the disease till 2023, only 10.5% included field-tested management practices and within those, only two reported solely positive impacts (Whiting-Fawcett et al. 2025). Thus, following the travel distance categories used in the present study, we advise washing caving equipment with water when changing subterranean sites situated up to 100 km apart and with water and soap for sites up to 1000 km apart. For longer distances, especially to different continents, we recommend using local equipment or following existing decontamination protocols such as those applied in North America or Australia. According to our study, the last should be particularly emphasized as a significant number of our respondents from Europe and Asia currently travel between continents without disinfecting or changing their equipment.

Considering the above, an effective campaign to prevent the anthropogenic spread of *Pd* should both provide knowledge and stimulate positive attitudes towards bat and cave conservation and make cleaning equipment more socially desirable and more easily feasible. In terms of attitudes, positive sentiments seem to be already prevailing: according to

our study, most cavers that have received information on the human impact on cave ecosystems have changed their behaviour accordingly; most cavers that had prior knowledge of WND agree that limiting its spread is needed and possible; and most cavers that follow WND-related decontamination protocols do so out of a sense of responsibility. This is not surprising as, according to the authors' rich caving experience, speleological activities are emotionally charged and cavers may think of the subterranean environment as their homeland. In terms of making field hygiene more socially desirable, we would suggest that a personal example could be particularly effective, especially when it comes from researchers who are known and respected within the community. Lastly, to make properly cleaning caving equipment more feasible, work in two directions is required. First, cavers that are unaware of WND and the related risks of pathogen pollution in caves, should be informed about the problem and its precise solutions. This is particularly needed in Europe and Asia where an up-to-date standardised protocol for cleaning and decontaminating caving equipment according to the travel distance has yet to be established and widely distributed. Importantly, these resources should be translated into each country's languages. Second, researchers, especially those involved in monitoring activities, should be incentivized to prioritize time for cleaning their equipment between sites and including more rest days between trips in different geographical regions. The success of this idea would mostly depend on the attitudes among the research community towards prioritizing stricter pathogen pollution prevention rather than obtaining faster results.

Last but not least, we advocate the need for further studies assessing caver's knowledge and attitude towards updated WND and cave conservation guidelines or going deeper into questions that we could not address in this paper. For example, we did not collect data on participants' sex, number of caving courses and workshops attended, or the exact type of science they practice in caves: all these are factors that might also influence hygiene habits. Additionally, our data might be slightly biased towards cavers that are involved in some kind of scientific activities as we distributed our survey partly through our personal contact networks containing a large number of colleagues; we also received a higher response rate from our team members' countries than from countries where we did not have personal contacts. Finally, the specific questions we used are only one of many ways to assess WND awareness and it has been observed that question formulation can influence statistical relations between knowledge and behaviour (Ajzen et al. 2011). Nevertheless, we believe that despite these limitations, the main points of our study remain valid. We hope that our questionnaire has raised even more interest in pathogen pollution in caves among our respondents and that cavers who wished to receive updates on our project would become valuable ambassadors spreading and improving our recommendations.

Conclusions

Pathogen pollution is a global problem that should be addressed via broad international cooperation. Thus, although significant advancements have been made in understanding and locally managing WND in severely affected areas, more efforts are

needed to prevent further long-distance introductions of its causative agent. Rising awareness among the caving community is an important step in this direction, yet it is not enough as other factors such as personal attitudes and the feasibility of the proposed conservation actions have stronger influence on human behaviour.

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Supplementary material 1

Survey questions

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Data type: docx

Link: https://doi.org/10.3897/subtbiol.52.140425.suppl1

Supplementary material 2

Organizations contacted to distribute the survey

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Data type: docx

Link: https://doi.org/10.3897/subtbiol.52.140425.suppl2

Supplementary material 3

***Pd* presence in respondents' countries according to published information prior to 2021 when our survey was conducted**

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Data type: docx

Link: https://doi.org/10.3897/subtbiol.52.140425.suppl3

Supplementary material 4

Number of respondents per country and continent

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Data type: docx

Link: https://doi.org/10.3897/subtbiol.52.140425.suppl4

Supplementary material 5

Consistency and change in cavers' hygiene habits across travel distances

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Data type: docx

Link: https://doi.org/10.3897/subtbiol.52.140425.suppl5

Supplementary material 6

Full output of the best model used to explain cavers' hygiene habits (expressed as biosecurity scores)

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Data type: docx

Link: https://doi.org/10.3897/subtbiol.52.140425.suppl6

Supplementary material 7

The R script used for the analysis

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Data type: R

Link: https://doi.org/10.3897/subtbiol.52.140425.suppl7

Supplementary material 8

Functions to load the necessary packages into the main R script

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Data type: R

Link: https://doi.org/10.3897/subtbiol.52.140425.suppl8

Supplementary material 9

Necessary packages to load into the main R script

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Data type: R

Link: https://doi.org/10.3897/subtbiol.52.140425.suppl9

Supplementary material 10

Original master data used for the analysis

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Data type: csv

Link: https://doi.org/10.3897/subtbiol.52.140425.suppl10

Supplementary material 11

Travel coordinates used to make Figure 6

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Data type: csv

Link: https://doi.org/10.3897/subtbiol.52.140425.suppl11